Global Ecology and Conservation 5 (2016) 12–21

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Original research article

A global assessment of current and future biodiversity vulnerability to habitat loss–climate change interactions

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ARTICLE INFO

Article history:
Received 9 November 2015
Accepted 9 November 2015
Available online 9 December 2015

Keywords:
Climate change
Habitat loss
Habitat fragmentation
Interaction
Synergy
Conservation
Biodiversity conservation

ABSTRACT

Habitat loss is the greatest threat to biodiversity and rapid, human-forced climate change is likely to exacerbate this. Here we present the first global assessment of current and potential future impacts on biodiversity of a habitat loss and fragmentation–climate change (HLF–CC) interaction. A recent meta-analysis demonstrated that the negative impacts of habitat loss and fragmentation have been disproportionately severe in areas with high temperatures in the warmest month and declining rainfall, although impacts also varied across vegetation types. We compiled an integrated global database of past, current and future climate variables and past vegetation loss to identify ecoregions where (i) past climate change is most likely to have exacerbated the impacts of HLF, and (ii) forecasted climate change is most likely to exacerbate the impacts of HLF in the future. We found that recent climate change is likely (probability >66%) to have exacerbated the impacts of HLF in 120 (18.5%) ecoregions. Impacted ecoregions are disproportionately biodiverse, containing over half (54.1%) of all known terrestrial amphibian, bird, mammal, and reptile species. Forecasts from the RCP8.5 emissions scenario suggest that nearly half of ecoregions globally ($n = 283$, 43.5%) will become impacted during the 21st century. To minimize ongoing and future HLF–CC impacts on biodiversity, ecoregions where impacts are most likely must become priorities for proactive conservation actions that avoid loss of native vegetation (e.g., protected area establishment). Highly degraded ecoregions where impacts are most likely should be priorities for restoration and candidates for unconventional conservation actions (e.g. translocation of species).

1. Introduction

Human-forced climate change and ongoing environmental degradation leading to habitat loss and fragmentation threaten the future of the world's biodiversity (Thomas et al., 2004; Hoffmann et al., 2010). The synergy between different

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http://dx.doi.org/10.1016/j.gecco.2015.11.002

threatening processes, whereby the presence of one exacerbates the effects of another, has been implicated in past biodiversity declines and extinction events (Lorenzen et al., 2011), yet little is known about how and where the interaction between habitat loss and fragmentation and climate change (hereafter, HLF–CC interaction) will impact ecosystems or species (Brook et al., 2008). This knowledge gap limits the identification of effective conservation responses in regions that have experienced, are experiencing, or are expected to experience both.

Previous spatial ecosystem assessments that have considered climate change have focussed on assessing the varying dimensions of potential exposure to climatic changes, including the temporal pace of climate change (Loarie et al., 2009), the degree of difference between past, current and predicted future climates (Ponce-Reyes et al., 2012; Watson et al., 2013), or the novelty of new climatic environments (Williams et al., 2007). These studies are important first-step assessments that identify those locations where climate change is likely to be most significant and raise awareness about its range of potential impacts. However, little attention has so far been given to potential interactions between climatic changes and other major anthropogenic processes that threaten biodiversity (Mantyka-Pringle et al., 2012; Watson and Segan, 2013). This is problematic because it is well established that most species that are imperilled or in a state of decline are simultaneously impacted by a range of threatening processes (Hilton-Taylor et al., 2009), with the predominant stressor being direct habitat loss and fragmentation (Brook et al., 2008; Hilton-Taylor et al., 2009).

The direct impacts of habitat loss and fragmentation (HLF) on biodiversity have been extensively documented and include extinction, decreased population abundance, reduced genetic diversity, lower reproductive success, lower dispersal ability, increased vulnerability to stochastic events, increased susceptibility to invasive species, simplified trophic structure and altered interspecies interactions (Fahrig, 2003; Fischer and Lindenmayer, 2007). Although already a widely distributed threat, HLF will continue to be a major pressure on species and ecosystem into the future (Newbold et al., 2015). There are several means by which rapid human-forced climate change may exacerbate or limit a species' ability to cope with HLF. For example, climate change induced behavioural changes have been implicated in reduced levels of individual fitness (Arponen et al., 2005), which may limit a species' ability to endure further habitat disruption. Climate change may also increase the distance a species needs to travel to locate suitable habitat in the event of future disturbance or loss (Williams et al., 2007). Climate change is also expected to increase the frequency and intensity of extreme events, such as heat waves, which may push populations already diminished by HLF over a tipping point as has been observed in some avian communities (McKechnie and Wolf, 2010).

Habitat loss and fragmentation may also limit or prevent species' adaptive responses to climate change, again resulting in more severe impacts. Species' adaptive responses to climate change are generally limited to three response mechanisms: a shift in range, a behavioural or physical change, and altered phenology (temporal shift in activity) (Bellard et al., 2012). Habitat loss and fragmentation may prevent or impair these responses. For example, habitat loss compromises a species' capacity for rapid dispersal or refugial retreat (Brook et al., 2008; Opdam and Wascher, 2004), while fragmentation may hinder a species' ability to track shifts in suitable environmental conditions or access remaining suitable habitat (Cushman, 2006). Habitat loss may also destroy microrefugia, localized climatically suitable areas in otherwise unsuitable landscapes, which provide species the opportunity to survive during unfavourable climate periods and locations from which to re-colonize when conditions become more suitable (Dobrowski, 2011; Scherrer and Körner, 2011). Even when there are no physical barriers to dispersal, a species' ability to navigate fragmented landscapes to seek out suitable areas may be lower than in intact landscapes due to reluctance to traverse unsuitable land cover types, leaving suitable habitat unoccupied because of a species failure to locate it (Opdam and Wascher, 2004). Populations whose range has been extensively lost or degraded may also lack the adaptive capacity (e.g. phenotypic plasticity or micro-evolution) to adapt to climate change *in-situ* because both their genetic and phenotypic diversity may have been reduced by declines in population size or connectivity (Jump and Peñuelas, 2005).

While it is clear that there are numerous mechanisms by which climate change and habitat loss and fragmentation could plausibly interact to magnify biodiversity impacts, few studies have documented HLF–CC impacts directly or examined how general or widespread they might be. Recently, however, Mantyka-Pringle et al. (2012) used a meta-analytic approach to detect adverse biodiversity impacts attributable to an HLF–CC interaction. Using a global assessment of 168 published data sets that examined the impacts of HLF on multiple taxa, they modelled the likelihood of observing a negative impact on biodiversity (decline in density, richness, diversity or probability of occurrence) due to HLF as a function of current climate and observed climate change (Mantyka-Pringle et al., 2012). They showed that negative impacts associated with HLF were more likely in landscapes with two key climatic determinants, (i) current high maximum temperatures and (ii) declining precipitation, and that the strength of the impact varied across different vegetation types but, with the exception of arthropods, varied little across taxa (Mantyka-Pringle et al., 2012). This is an important study because for the first time it enables the spatial assessment, and hence preliminary risk assessment, of where the HLF–CC interaction is most likely to impact biodiversity.

Here, we apply the models derived in the Mantyka-Pringle et al. (2012) meta-analysis to an integrated set of global spatial data comprising vegetation loss, current climate, observed climate change, and forecasted climate change (using RCP 4.5 and 8.5 scenarios to both 2055 and 2090 IPCC, 2013) to identify ecoregions where an HLF–CC interaction is most likely to (1) have already impacted biodiversity, and (2) cause biodiversity impacts in the future as a result of future HLF and/or climate changes. Understanding where HLF–CC interactions will most impact biodiversity is an important step towards effectively allocating conservation resources aimed at preventing ongoing biodiversity loss.

2. Methods

2.1. Ecoregional data

Following previous global analyses (e.g. Watson et al., 2013, Funk and Fa, 2010, Iwamura et al., 2010) we used the global ecoregions ($n = 825$) identified by Olson et al. (2001) as the basis for our analysis. Ecoregions represent relevant environmental and ecologically distinct spatial units at the global scale (Olson and Dinerstein, 2002) and are used by international funding institutions and conservation organizations to guide global conservation investments, assessments and actions (Watson et al., 2013; Funk and Fa, 2010).

We reclassified each ecoregion to match one of the seven broad vegetation types (forest, rainforest, savanna, shrubland, wetland, woodland and other) used in the meta-analysis of Mantyka-Pringle et al. (2012) (Table S1, Fig. S1). Mantyka-Pringle et al. (2012) classified a broad group of vegetation types as "other", including salt marshes, meadows, pastures, coastal sage scrub and coastal dunes. Given the diversity within this group, and the consequent diversity anticipated in their responses to climate change and HLF, we excluded all of these ecoregions ($n = 109$) from our analysis. We also followed Iwamura et al. (2010) and excluded ecoregions that were not fully covered by all climate data sets ($n = 64$) as well as the 'Rock and Ice' and 'Lake' ecoregions ($n = 2$), leaving 650 ecoregions for analysis (Fig. S1).

2.2. Vegetation assessment within ecoregions

Following previous studies (e.g. Watson et al., 2013), we used a conservative measure of the degree of degradation in an ecoregion by quantifying the proportion of areas where native vegetation had been totally transformed through agricultural development or urbanization. This was achieved using the GlobCover version 2.1 dataset, a global land cover classification model at ~300 m spatial resolution (Arino et al., 2008). The GlobCover dataset defines 65 land cover types categorized into Cultivated Terrestrial Areas and Managed Areas, Natural and Semi-natural Terrestrial Vegetation, Natural and Semi-natural Aquatic Vegetation, Artificial Surfaces and Associated Areas, and Inland Water Bodies. All areas classified as Cultivated Terrestrial Areas and Managed Lands, Artificial Surfaces and Associated Areas, were treated as 'modified' cover types, with all other cover types defined as 'intact'. We calculated both the total area and modified area of each ecoregion to determine the proportion of native vegetation lost in each (E_{modified}). We used the global median for ecoregional loss of native vegetation ($E_{\text{modified}} = 28.4\%$) to categorize ecoregions as either highly degraded ($E_{\text{modified}} > 28.4\%$) or relatively intact ($E_{\text{modified}} < 28.4\%$).

2.3. Climate data

The Mantyka-Pringle et al. (2012) meta-analysis found that four climate variables could be used to assess where the impacts of HLF were most likely to be exacerbated by climate change; (1) $T_{\max}$—maximum temperature of warmest month, (2) ΔP—change in precipitation, (3) ΔT—change in temperature, and (4) $P_{\min}$—precipitation in the driest month. While all four variables were identified as important, high maximum temperatures in the warmest month and declining precipitation (Mantyka-Pringle et al., 2012) were the most influential.

Like Mantyka-Pringle et al. (2012), we derived the current climate variables ($T_{\max}$, $P_{\min}$) from the WorldClim database at ~1 km^2 resolution, which provides an average over the period from 1950 to 2000 (Hijmans et al., 2005). Also following Mantyka-Pringle et al. (2012) we calculated the observed change in climate variables (ΔP_{2010}, ΔT_{2010}; negative values indicate declines) from the Climatic Research Unit (CRU) time-series version 3.20 observed climate database at the University of East Anglia (1901–2010) (Mitchell and Jones, 2005) as the difference between the mean in the most recent period (1981–2010) and the earliest period available (1901–1930).

To assess future climate conditions, we used Representative Concentration Pathways (RCP) 4.5 and 8.5 and the ensemble median forecast from 26 general circulation models (GCMs) in two future time periods 2046–2065 and 2081–2100 (Girvetz et al., 2009). RCP 4.5 is an intermediate emission scenario that is based on stricter climate policy and low energy use going forward, in which CO_2 emissions begin declining by 2040 and total radiative forcing of all human greenhouse gas emissions stabilize just after 2100. RCP8.5 is a higher range emission scenario consistent with high population growth, no climate policy change, and continued reliance on fossil fuels (Van Vuuren et al., 2011). Ensemble forecasts were used because they show better large scale agreement with observed data (Meehl et al., 2007), have been used for global studies (Loarie et al., 2009), and have been suggested to be more appropriate for biological risk assessments (Fordham et al., 2011). Change in precipitation and temperature in each time period (ΔT_{2055}, ΔT_{2090}, ΔP_{2055}, ΔP_{2090}) was calculated by subtracting the mean annual value in the earliest period available (1901–1930) from the value forecasted in the future time period (2055, 2090; negative values indicate declines). In addition to the ensemble median forecast we also considered upper (ΔT_{2055U}, ΔT_{2090U}, ΔP_{2055U}, ΔP_{2090U}) and lower (ΔT_{2055L}, ΔT_{2090L}, ΔP_{2055L}, ΔP_{2090L}) bound GCM forecasts for change in precipitation and temperature to assess the likelihood of HLF–CC impacts against the range of possible future conditions. Upper bound estimates (worst case scenario) were derived by using the minimum forecast for precipitation (driest) and the maximum forecast for temperature (warmest) from any of 26 GCMs in both future time periods. Lower bound estimates (best case scenario) were derived by using the highest precipitation forecast (wettest) and minimum forecast for temperature (coolest) from any of 26 GCMs in both future time periods.

2.4. Analysis

We evaluated the probability of observing a negative HLF–CC impact on biodiversity by applying vegetation type-specific model average coefficients derived as part of the Mantyka-Pringle (2012) study (Mantyka-Pringle pers comm) to our integrated vegetation and climate datasets. When no single model is clearly superior (AIC weight > 0.9), the use of model average coefficients can reduce model selection bias and is preferable to selecting the best model for inference (Burnham and Anderson, 2002). We used the mean values for each variable (T_{max}, P_{min}, $E_{modified}$, ΔP_{2010}, ΔT_{2010}, ΔT_{2055}, ΔT_{2090}, ΔP_{2055}, ΔP_{2090}) within each ecoregion for analyses. Following Mantyka-Pringle (2012) we standardized each predictor variable to have a mean of zero and standard deviation of one.

We first evaluated current levels of risk based on current conditions (T_{max}, P_{min}, $E_{modified}$) and observed climate change (ΔP_{2010}, ΔT_{2010}). We then forecasted risk in two future time periods (2055, 2090) by using forecasted change in temperature and precipitation (ΔT_{2055}, ΔT_{2090}, ΔP_{2055}, ΔP_{2090}). We characterize the forecasted probability of observing HLF–CC impacts in an ecoregion following the most recent Intergovernmental Panel on Climate Change (IPCC) report; "Unlikely" (<33% probability), "About as likely as not" (33%–66%), "Likely" (>66%), and "Very likely" (>90% probability) (IPCC, 2013).

Temporal change in ecoregion vulnerability was assessed by defining transition states with respect to the current likelihood of HLF–CC impacts and likelihood in a future period (2055 or 2090). We simplified the categories used above and classified an ecoregion as "At-risk" in the time period if the probability of HLF–CC impacts was >66%, and "Low-risk" if the probability was <66%. Classification from the two time periods was combined to develop the vulnerability trajectory for each ecoregion, referred to as its transition state. For example, a transition state of 'At-risk → At-risk' means that the probability of HLF–CC impacts is currently >66% and is expected to stay >66% in the future time period. Four transition states were possible with respect to any future time period, (1) At-risk → At-risk, (2) At-risk → Low-risk, (3) Low-risk → At-risk and (4) Low-risk → Low-risk.

3. Results

3.1. Current interaction risk

Our results indicate that HLF–CC impacts on biodiversity as a result of climatic change during the 20th century were likely (probability $>$ 66%) in 120 (18.5%) ecoregions, and very likely (>90% probability) in 12 (1.8%) ecoregions (Fig. 1). A negative impact was "as likely as not" (probability 33%–66%) in 475 (73.1%) ecoregions assessed, and unlikely (probability $<$ 33%) in only 55 (8.5%) ecoregions. A weak, but significant, negative correlation was found between $E_{modified}$ and the probability of HLF–CC impacts across all ecoregions (Pearson's $r(648) = -0.20$, $p < 0.01$), suggesting that many of the ecoregions most sensitive to HLF–CC impacts may not yet have been impacted because they are currently relatively intact. Impacted ecoregions were also disproportionately biodiverse (Wilcoxon rank-sum test $w = 45\,979$, $p < 0.01$). Median richness of four taxa (amphibians, birds, mammals, reptiles) in the ecoregions where impacts were likely was 527 (IQR 351-719) (cf. global median, 406 (IQR 307-630)) (SI Text).

Rainforests, savannas, shrublands and wetlands were the most vulnerable vegetation types, with HLF–CC impacts likely in nearly half (45.3%) of rainforests, a third (33.3%) of savanna, almost a third (29.3%) of shrublands and all (100%) wetland ecoregions. Rainforest and savanna ecoregions account for 29.8% of ecoregions globally, but represented 63.3% of all ecoregions that are likely to have been impacted (Fig. 2, Fig S2). Rainforests alone accounted for over a third of all ecoregions identified where HLF–CC impacts as a result of past climate change were likely (Fig. S2). In contrast, HLF–CC impacts were least likely in forest and woodland ecoregions, which together account for 60.1% of ecoregions considered in the analysis, but only 16.7% of ecoregions where impacts are likely (Fig. 2, Fig. S2).

3.2. Forecasted interaction risk

Median GCM forecasts based on the RCP 4.5 scenario suggested that the number of ecoregions where impacts are likely will decrease slightly to 113 (17.4%) in 2055, from 120 (18.4%) today, before increasing to 122 (18.7%) in 2090 (Figs. S3 and S4). While median forecasts from the higher emissions RCP 8.5 also predicted a decrease in 2055 to 111 (17.0%), the RCP 8.5 scenario departed markedly from the RCP 4.5 scenario in 2090, where it was suggested that the number of ecoregions where impacts are likely will increase to 170 (26.1%) (Table S2, Figs. S5 and S6).

All forecasts suggested a substantial shift in the composition of vegetation types most likely to be impacted. Savanna, wetlands, and to a lesser extent forests, became more vulnerable, while HLF–CC impacts were forecasted to be less likely in rainforests, woodlands and shrublands (Fig. 3, Fig. S2). By 2055, median GCM forecasts indicated that savanna and wetland ecoregions will account for all ecoregions where impacts are very likely (>90% probability) (Fig. 3). The reduction in the likelihood of HLF–CC impacts in woodlands was robust to choice of RCP and future assessment period, with all woodland ecoregions classified as unlikely to experience impacts in both future time periods and in both RCP4.5 and RCP8.5 (Fig. 3).

Assessing the temporal trajectory of ecoregion vulnerability shows that the total number of ecoregions that are currently at-risk of HLF–CC impacts or will become at-risk (>66%) to HLF–CC impacts in future ranged from 153 (23.5%), using the most optimistic emissions forecast, to 283 (43.5%) in the least optimistic emissions forecast (Fig. 4). Impacted ecoregions

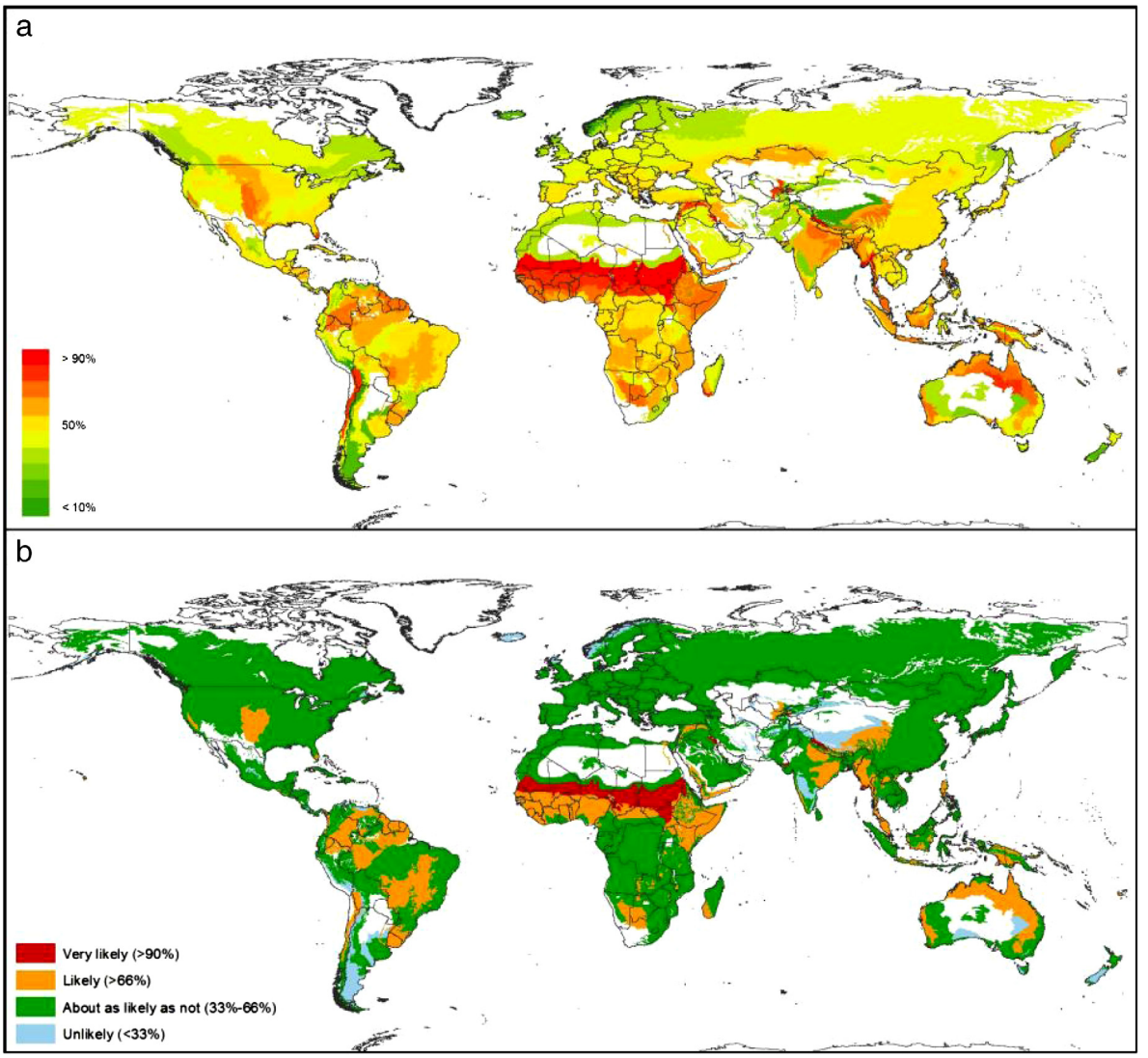

Fig. 1. Likelihood that observed climate change has exacerbated the impact of habitat loss and fragmentation on biodiversity at ecoregional scale based on (a) raw probability, and (b) confidence intervals following IPCC (2013). Probability of HLF–CC interactions was assessed as a function of five parameters using vegetation type-specific model average coefficients from Mantyka-Pringle et al. (2012). Ecoregions in white were excluded from the assessment because they did not conform to the selected broad vegetation categories or because they were not sufficiently covered by climate data.

were more species rich than ecoregions globally in both the most and least optimistic scenarios (RCP 4.5: median richness of impacted ecoregions $= 486$, median richness of ecoregions globally $= 406$, Wilcoxon rank-sum test $w = 55\,054$, $p < 0.05$; RCP8.5: median richness of impacted ecoregions $= 489$, $w = 103\,016$, $p < 0.01$) (SI Text).

Variability in the number of at-risk ecoregions was primarily driven by variation in the number of ecoregions classified as low-risk today that were forecasted to be at-risk in the future, which ranged from 33 (5.1%) ecoregions in the most optimistic forecast to 163 (25.1%) in the least optimistic forecast (Fig. 4). In contrast, we found little variation in the number of ecoregions forecasted to be at-risk in both time periods or to transition from at-risk today to low-risk in the future (Fig. 4). Overlaying loss of native vegetation onto ecoregional transition states we find that the majority (60%) of ecoregions identified as At-risk $\rightarrow$ At-risk are relatively intact today, while ecoregions identified as either At-risk $\rightarrow$ Low-risk or Low-risk $\rightarrow$ At-risk were almost equally distributed between relatively intact and modified (Fig. 5).

4. Discussion

This is the first global assessment of where an interaction between habitat loss and fragmentation and climate change (HLF–CC interaction) is most likely to have impacted biodiversity in the recent past and to forecast where these impacts are most likely to occur in future. We find that HLF–CC impacts are likely (>66% probability) to have occurred in 120 (18.5%)

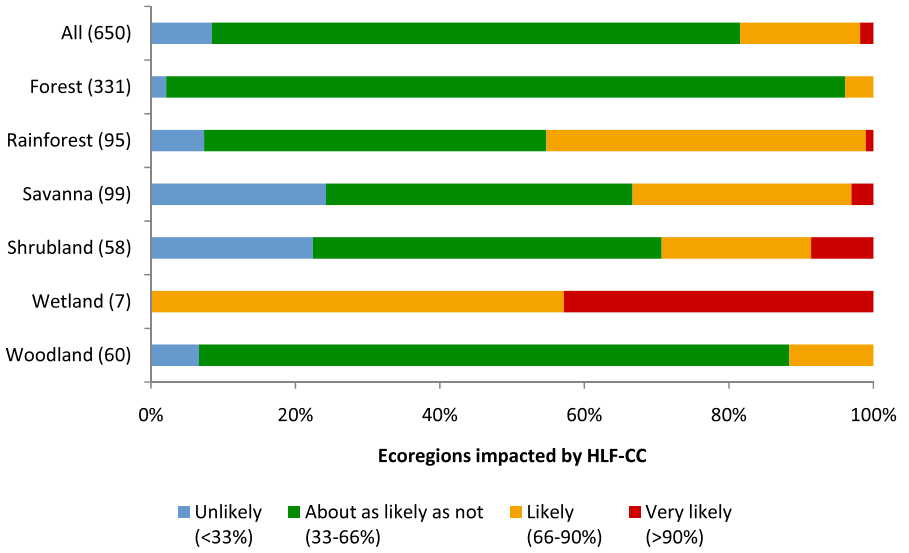

Fig. 2. Present day confidence intervals for the likelihood of observed climate change exacerbating the impact of habitat loss and fragmentation (HLF). The proportion of ecoregions in the confidence interval is indicated by the *x*-axis, and vegetation types along with the number of ecoregions in the vegetation type listed in parenthesis on the *y*-axis. Probability of HLF–CC interactions was assessed as a function of five parameters using vegetation type-specific model average coefficients from Mantyka-Pringle et al. (2012).

ecoregions as a result of climate changes that have occurred in the 20th century, while as many as 283 (43.5%) ecoregions may become impacted over the course of the 21st century. In interpreting the management implications of our results, we make a broad distinction between ecoregions where HLF–CC impacts are likely that have already experienced extensive clearing of native vegetation (hotspots for probable past HLF–CC impacts and thus candidates for restoration management actions) and those in which native vegetation remains largely intact (hotspots for potential future HLF–CC impacts if habitat is degraded and thus candidates for protection management actions). Relative priorities within these groups can be refined with respect to how biodiversity vulnerability to HLF–CC impacts is likely to change as a result of forecasted climate change.

We identify 66 relatively intact ecoregions where climate change to date is likely to exacerbate biodiversity losses if their intactness is compromised. By the end of the century, our models suggest that forecasted climate changes will result in a ∼50% increase in the number of ecoregions in this risk category to 92. These are ecoregions where the impact of future HLF on biodiversity will be magnified by climate change. Ensuring the continued intactness of native vegetation in these ecoregions should become a conservation priority. Increasing the protected area coverage is the most obvious management strategy to limit HLF–CC impacts, as protected areas are often a good mechanism to maintain vegetation integrity (Andam et al., 2008) and is consistent with the Convention on Biological Diversity (CBD) Aichi Targets (CBD, 2011). Other regional strategies include the introduction and acceptance of conservation-compatible development (Woinarski, 2007) and payment for ecosystem service (PES) programs such as REDD+ that are aimed at ensuring natural systems are retained by offering compensation for the services they provide that would be lost if converted to other land uses (Miles and Kapos, 2008; Gullison et al., 2007).

The ecoregion transition states that we developed to summarize expected changes in vulnerability (Figs. 4, 5) provide additional information that will help aid prioritization of resources between ecoregions and to promote learning. The 41–50 (6.3%–7.7%) ecoregions identified as At-risk → At-risk are the highest priority for preventing loss of native vegetation because the impact of that loss is likely to be exacerbated by climate change. The majority of At-risk → At-risk ecoregions are currently relatively intact, which represents a clear opportunity to mitigate HLF–CC impacts in many of the ecoregions that are persistently vulnerable. In contrast, the 367–497 (56.5%–76.5%) ecoregions where impacts are unlikely now and in the future (Low-risk → low-risk) are lower priorities for conservation action aimed at preventing HLF–CC impacts.

Targeting conservation action to minimize HLF–CC impacts in ecoregions expected to transition between risk states (At-risk → Low-risk and Low-risk → At-risk) is more nuanced. In At-risk → Low-risk ecoregions climate forecasts indicate the likelihood of HLF–CC impacts will decrease in the future. This suggests that clearing today will expose these ecoregions to greater HLF–CC impacts than clearing in the future. Thus conservation action that delays (even if it does not ultimately prevent) loss of native vegetation in these ecoregions may benefit biodiversity because loss at a later date is less likely to be accompanied by HLF–CC impacts. In contrast, climate change is expected to increase the probability of HLF–CC impacts in Low risk → At-risk ecoregions, indicating alternative priorities in these ecoregions. The first is monitoring climatic changes and re-assessing risk as new data become available. Where climate change increases risk as expected, prevention of loss and restoration will become more urgent priorities. Second, significant restoration efforts in highly degraded Low risk → At-risk

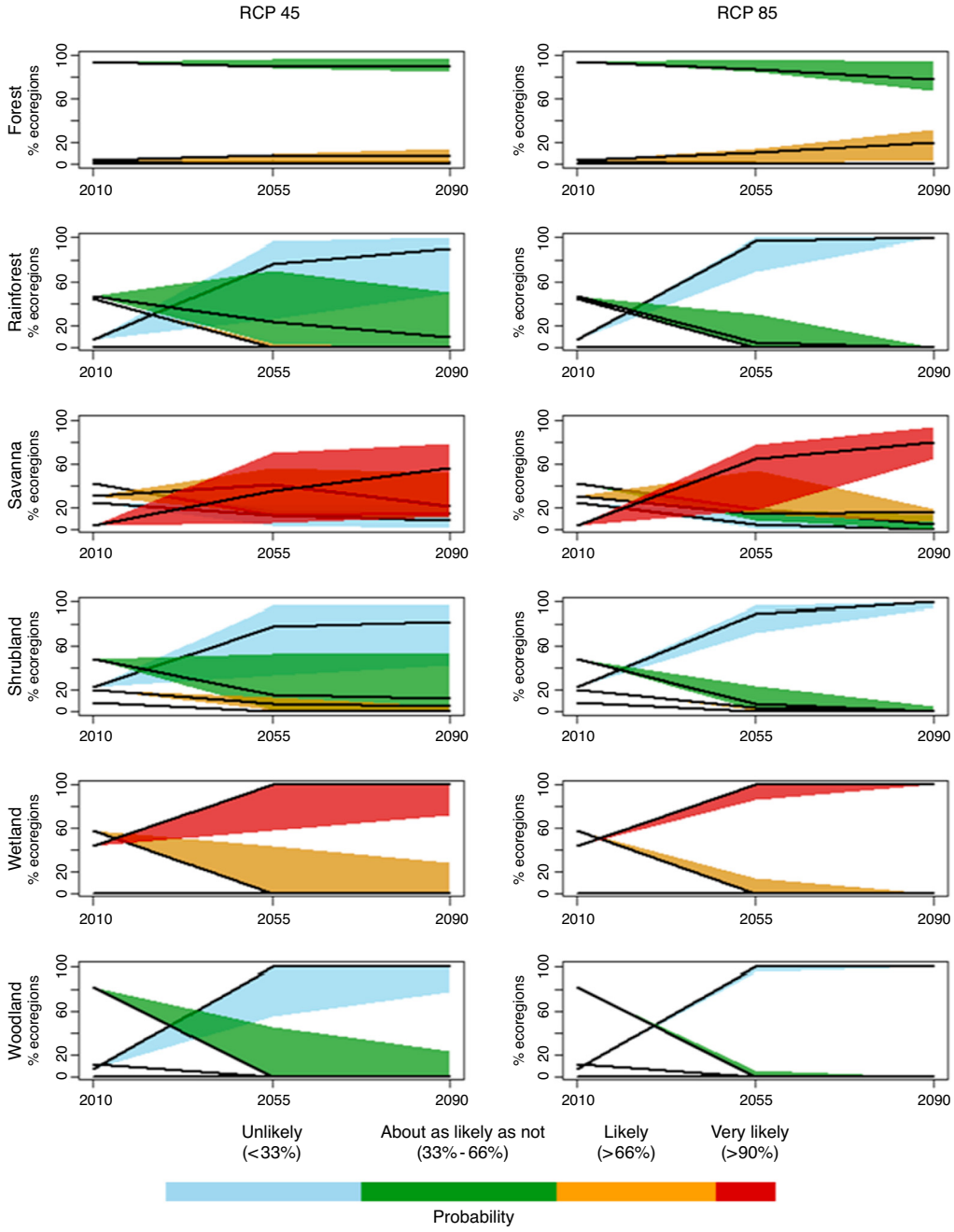

Fig. 3. Forecasted change in ecoregion vulnerability to habitat loss and fragmentation–climate change (HLF–CC) interaction impacts. Solid black lines indicate probability based on GCM median forecasts (IPCC, 2013). The width of the shaded band represents the variance in the proportion of ecoregions in the probability class between the upper and lower bound GCM. Narrower shaded bands indicate greater GCM agreement. Probability of HLF–CC interactions was assessed as a function of five parameters using vegetation type-specific model average coefficients from Mantyka-Pringle et al. (2012).

ecoregions before climatic changes make HLF–CC impacts more likely may spare local biodiversity from the interaction between the two drivers.

The ecoregion transition states may also serve as an additional resource to assess the efficacy of different conservation interventions as tools to deal with HLF–CC impacts (Figs. 4, 5). Ecoregions where the likelihood of HLF–CC impacts is expected to change most dramatically may offer a unique opportunity for observing and monitoring changes as they occur (Figs. S9 and S10). These ecoregions are also potential laboratories for adaptive management experiments that could provide insights into how best to deal with the challenges climate change poses for biodiversity in the 21st century (Pullin and Knight, 2009).

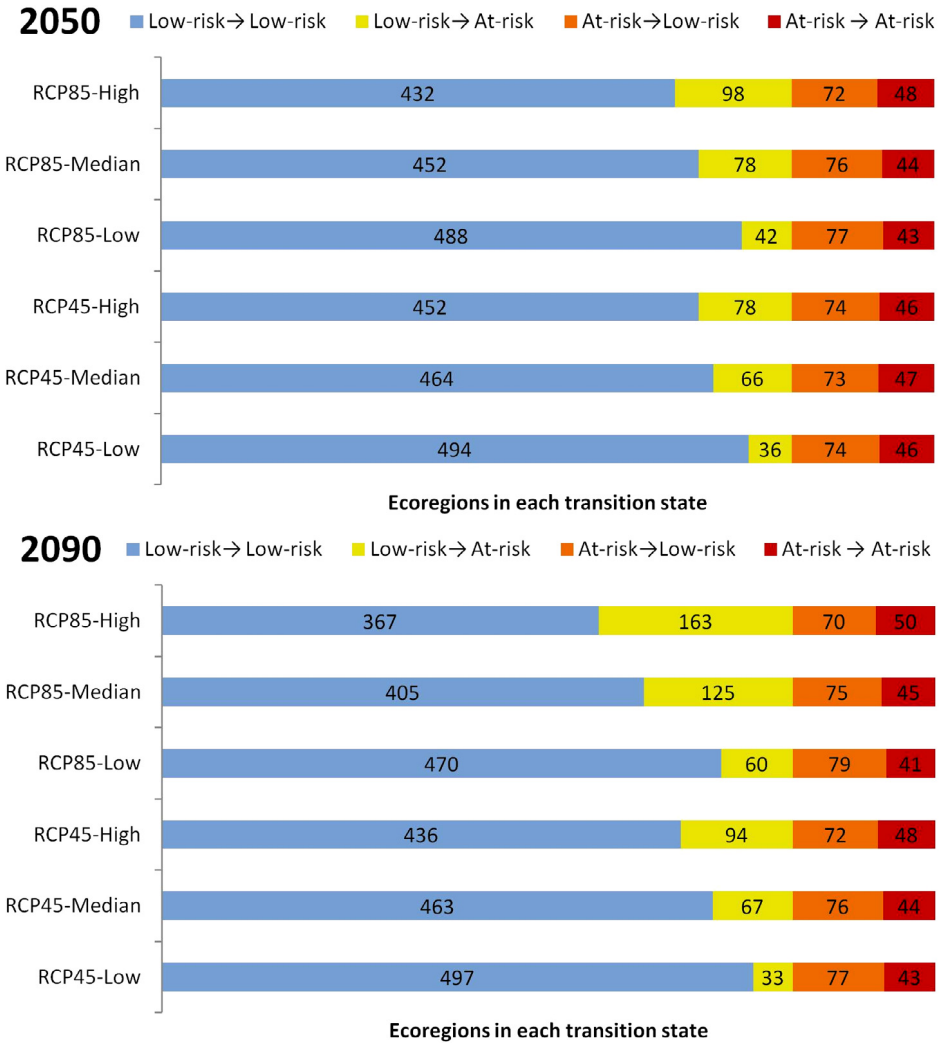

Fig. 4. Forecasted change in ecoregion vulnerability to habitat loss and fragmentation–climate change (HLF–CC) interaction impacts. Transition states were defined based on the ecoregion's current and forecasted future vulnerability to HLF–CC impacts. We followed IPCC thresholds for what is 'likely' (defined as >66% probability): if the probability of HLF–CC impacts in the time period was <66% the ecoregion was classified as 'low-risk' and if HLF–CC impacts were >66% the ecoregion was classified as 'At-risk'. Likelihood of HLF–CC impacts was independently evaluated in each time period and then combined to develop the transition state. For example, a transition state of 'At-risk → At-risk' means that the probability of HLF–CC impacts is currently >66% and is expected to stay >66% in the future time period.

Several caveats should be acknowledged in this preliminary spatial assessment of the potential impacts from HLF–CC interactions. First, impacts on individual species cannot be inferred from ecoregional vulnerability. The extent to which individual species in the ecoregions identified here will be impacted by the synergy between habitat loss and climate change will to some degree be mediated by species' ecological and biological traits (e.g., fecundity, population dynamics, behaviour, interspecific interactions Murray et al., 2014). Understanding how individual species and systems will respond to HLF–CC is thus likely to be more context specific and clearly warrants additional research attention. Second, while the evidence base developed by Mantyka-Pringle et al. (2012) is an important step towards assessing broad trends across a range of vegetation types, more research is needed to tease out the mechanisms of HLF–CC impacts and to resolve questions around the direction and magnitude of responses across different vegetation types and taxa. For example, their findings suggest that additional warming may reduce the likelihood of HLF–CC impacts in rainforest, woodland and shrubland systems (Mantyka-Pringle et al., 2013). The finding for rainforests, for example, seems at odds with other work on the sensitivity of rainforests to climate change and the interaction between those changes and clearing of native vegetation, which generally suggest that clearing increases risk (Malhi et al., 2009; Corlett, 2011). Such differences highlight the need to generate testable mechanistic hypotheses such that future research can better assign causality where HLF–CC interactions are associated with observed biodiversity impacts. Third, we also note that the (Mantyka-Pringle et al., 2012) meta-analysis was based on observed climatic changes during the 20th century, while changes in the 21st century are expected to be significantly larger.

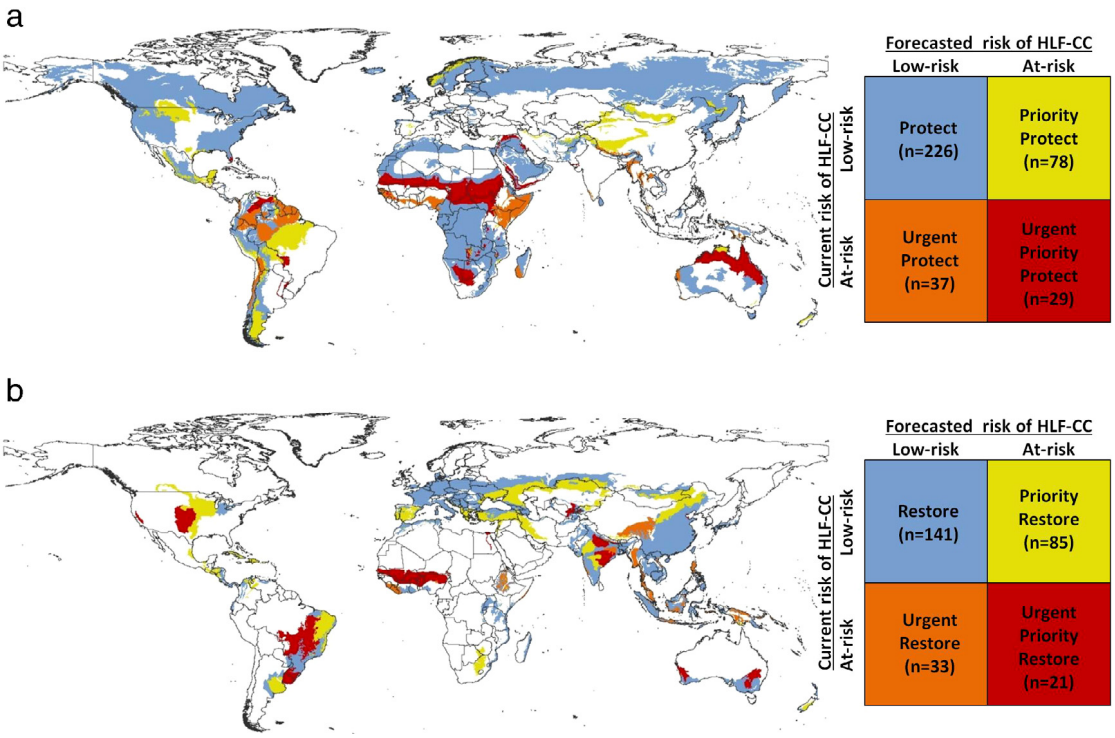

Fig. 5. Ecoregional intactness and forecasted trajectory of vulnerability to habitat loss and fragmentation–climate change (HLF–CC) interaction impacts. Colours indicate relative priority with respect to avoiding HLF–CC interaction impacts and are based on the trajectory of ecoregion vulnerability to HLF–CC interaction impacts outlined in Fig. 4. Future vulnerability assessed using the forecasted climate in 2090 based on RCP 8.5. Panels indicate likely focus of management activities, based on ecoregion intactness, (a) protection of relatively intact ecoregions, or (b) restoration in highly ecoregions. Ecoregions were classified as relatively intact or highly degraded with respect to the global median for modification ($E_{\text{modified}} = 28.4\%$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The magnitude of future climate change may thus fall outside the range used to establish the HLF–CC impact relationship in many regions.

Despite these challenges, using an empirical evidence base to assess ecoregion vulnerability to HLF–CC impacts represents an important, data-driven advance in understanding the potential risks posed by both climate change and HLF. By accounting for the non-linearity in system responses to these two stressors, we are able to identify areas where the biodiversity benefit of prevented loss or restoration of native vegetation are more likely to be magnified by the simultaneous avoidance of the interaction with climate change. This is important for both efficiently prioritizing actions (Joseph et al., 2009; Evans et al., 2011) and evaluating their effectiveness (Andam et al., 2008), and is a critical step towards resolving the longer-term uncertainties around future climate change, its effects on biodiversity, and how different conservation actions can be targeted to address this challenge.

Acknowledgements

We thank Liana Joseph, Molly Cross, Jonathan Rhodes, Piero Visconti and Chrystal Mantyka-Pringle for their thoughtful comments and discussion. We also thank Chrystal Mantyka-Pringle and her co-authors for their willingness to share data and methods from their work.

Appendix A. Supplementary data

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.gecco.2015.11.002.

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